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Modeling grapevine performance with 'VitiSim', a weather-based carbon balance model: Water status and climate change scenarios

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ABSTRACT

A carbon balance model (VitiSim) was used for assessing the effects of vine water status and different climate scenarios on the dry matter production and partitioning of 'Tempranillo' grapevines (*Vitis vinifera* L.) grown in two different Spanish regions. Inputs included weather daily variables, stem water potential measurements and vineyard system data. Partitioning is based on the supply and demand balance using relative sink strength coefficients when carbon supply is lower than organ demands. A new routine to consider the effect of vine water status on photosynthesis rate was implemented in the model. Experimental data from two Spanish locations, several seasons (2007–2011) and well-watered and water-stressed vines were used for validating the model. A sensitivity analysis showed that model outputs are greatly influenced by those inputs linked to light interception. Simulated dry matter productions were realistic even though in general the amounts were underestimated. VitiSim was able to reproduce the effect of water stress on dry matter production observed in the field. Then, the model was used to estimate vine dry mass in different locations within Spain and worldwide under the standard current meteorological condition and under two climate change scenarios. Results were in accordance with those commonly found in field studies. Hence, this model appears useful to estimate vine dry matter potential from few easily available inputs and to simulate the effects of deficit irrigation strategies on grape yield. Further routines must be implemented to enhance VitiSim predictive capabilities and reliability.

1. Introduction

A great number of interrelated factors (including photosynthesis, location of competing sinks, storage capacity and transport) control carbon partitioning in woody plants such as grapevines (*Vitis vinifera* L.). Environmental factors (e.g. water stress) and cultivation practices, including irrigation, might modify this carbon balance and affect fruit size, quality and yield (Deloire et al., 2004; Poni et al., 2018). In addition, climate change will alter meteorological conditions in the near future and this might affect grape yields and grape composition for high-quality wine production (Fraga et al., 2016; Maxwell et al., 2015). Furthermore, the response from several cultivars to these factors might be different; hence, the complexity of carbon partitioning in vines increases (Palliotti et al., 2014).

In order to cope with this complexity, models are useful tools to understand carbon balance in woody plants (Lescourret et al., 2011; Pallas et al., 2016) and might allow scientists to assess the effects of cultivation practices on this balance. In general, a comprehensive crop model should fulfill the following desirable and concurrent features: i) parsimony in data input; ii) high degree of user-friendliness in terms of usability and output visualization and interpretation; iii) reasonable accuracy of produced outputs and, iv) a broad output spectra covering plant growth, ripening and dry matter production and partitioning (Cola et al., 2014). Ideally, a model should be accessible, understandable and useable by those other than the model developers.

Many models have been developed for assessing plant growth and physiology, and they have been adapted to different crops (e.g. Grossman and DeJong, 1994; Lescourret et al., 2011). In the case of grapevines, there are models which accurately predict specific processes such as phenology (Fila et al., 2012), vegetative growth and yield (Bindi et al., 1997), leaf age, foliage density and canopy light interception and distribution (Louarn et al., 2008), sugar accumulation (Dai et al., 2009), carbon assimilation and allocation (Vivin et al., 2002). Nevertheless, these models do not comprehend all the desirable features listed above.

Grapevine in commercial production can be a difficult subject for modeling due to the extreme manipulations by growers such as variable pruning, training, shoot selection, canopy shoot positioning, leaf

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removal, hedging, cluster thinning, etc. These practices are effective agriculturally, but disrupt many of the natural growth habits and allometric relationships that underpin most plant models. Moreover, almost every vineyard has a unique combination of natural and managed factors. Thus modeling grapevines should not attempt excessively detailed simulations as results will have limited value to other conditions.

A model for predicting seasonal dry matter production in apple (Lakso et al., 2001) was used as a basis for assessing leaf area and daily carbon balance and dry matter accumulation in grapevines (Lakso and Poni, 2005; Poni et al., 2006). This approach proved to be simple, easy to use and provided quite fair estimations of leaf area, dry matter and carbon balance, proving its usefulness for simulating carbon exchange in vines (Poni et al., 2006; Lakso et al., 2008).

The aim of the current study was to improve an existing model of carbon balance in grapevine (Poni et al., 2006; Lakso et al., 2008) in order to take into account the effect of water stress and irrigation. Moreover, the model was tested with experimental data from vineyards (*Vitis vinifera* L. cv. 'Tempranillo') from two different Spanish regions. In addition, a sensitivity analysis was carried out for determining the inputs that exert the greatest influence on model outputs. Furthermore, the model was used to estimate dry mass accumulation of a standard vineyard located in different sites within Spain and worldwide as well as for simulating the effects of two different climate change scenarios on grapevine carbon balance.

2. Materials and methods

2.1. Plant material and experimental data

Field data came from experiments carried out in two Spanish locations (Supplementary Fig. 1), chosen on the basis of data availability: Badajoz (Extremadura, W Spain) and Requena (Valencia, E Spain). The vineyards studied were planted with 'Tempranillo'. Detailed descriptions of the study sites and irrigation treatments can be found in Picón-Toro et al. (2012) for Badajoz and Intrigliolo et al. (2012) for Requena. Therefore, only a brief description of each site is provided here.

The Badajoz vineyard was located in the research farm "Finca La Orden" (38° 51′ N, 6° 40′ W, elevation 198 m). Tempranillo vines were planted in 2001 and grafted onto Richter 110 at a spacing of 2.5 m by 1.2 m. Vines were trained to a vertical trellis on a bilateral cordon system oriented in the East-West direction. Vines were pruned to eight spurs and two buds per spur. The soil at this site had a silt-loam texture, with scarce calcium and low organic matter content, water holding capacity was 160 mm m^{-1}. Rooting depth was approximately 1.6 m. Climate is Mediterranean with mild Atlantic influence, dry hot summers and cold winters with irregular precipitations (470 mm annual average). In this case, the treatments considered were rain-fed and irrigation to replace 100% of crop evapotranspiration (Picón-Toro et al., 2012).

The vineyard located near Requena (39° 29′ N, 1° 13′ W, elevation 750 m) was planted in 1991 with Tempranillo vines on 161–149 rootstock at a spacing of 2.45 by 2.45 m. Vines were trained to a vertical trellis on a bilateral cordon system oriented in the North-South direction. The soil at this site had a clay loam to light clay texture, was highly calcareous and of low fertility, water holding capacity was 180 mm m^{-1}. Rooting depth was 2 m, approximately. Climate is continental with average annual rainfall of 430 mm of which about 65% falls during the dormant period. In this vineyard, rain-fed plants and those irrigated to the 75% of the estimated crop evapotranspiration were considered (Intrigliolo et al., 2012).

The period of study depended on the site: for Badajoz it was from 2007 to 2011 (5 years) and for Requena it was from 2008 to 2009 (2 years).

2.2. Field determinations for input data

Climate data (including maximum and minimum air temperature, rainfall, relative humidity, wind speed and solar radiation) were daily collected at weather stations located close to the experimental vineyards. These data allowed for computing vapor pressure deficit (VPD) and potential evapotranspiration (ET_0, Allen et al., 1998).

Over the growing season, midday stem water potential (Ψ_s) was measured in order to assess vine water status (Choné et al., 2001). Hence, Ψ_s readings were performed with a pressure chamber (Soil-Moisture Corp., Santa Barbara, USA) on three representative vines per replicate and one leaf per plant (9 readings per treatment). Measurements were carried out at midday (12:00–13:00 h) under sunny conditions on bagged leaves at 2-week intervals. Leaves were covered with a plastic bag and aluminum foil for at least 1 h prior to the measurements (Choné et al., 2001). At flowering, fruit set and veraison stages, the proportion of solar radiation intercepted by vine canopy was assessed in both sites using a ceptometer (LP-80, AccuPAR, Decagon Devices, Pullman, WA, USA). In order to obtain the curve of solar radiation proportion intercepted by the canopy over the growing season, the measured values were linearly interpolated between dates.

A dry mass evaluation of each plant organ (leaves, shoots and fruits) except roots (vines could not be sacrificed in the test vineyards) was carried out. Although the root systems of mature cropping vines may be large, the fraction of seasonal dry mass that is partitioned to them is often very small and the great majority remaining in the new seasonal growth (Bates et al., 2002). At harvest, all clusters from five plants per treatment were taken, weighed and dried in an oven at 65 °C till constant weight. Leaves from the same plants were removed and dried in the same conditions. At winter, vines were pruned and shoots were dried and weighed.

2.3. Model overview

'VitiSim' is a model for describing seasonal dry matter production of a grapevine that was originally developed for apple trees (Lakso and Johnson, 1990), modified over time (Lakso et al., 2001) and adapted to grape (Lakso and Poni, 2005; Lakso, 2006; Lakso et al., 2008). The model runs at a daily time-step in order to simplify the requirements for weather data and the complexities of diurnal radiation/canopy geometry. Also for simplicity the model uses the "big leaf" approach of combining individual organs, such as shoots or fruit, into a few super organs. It is assumed to be one leaf (canopy), one fruit (crop), one woody structure and one root made up of the population of individuals which may vary their numbers or activity. Previous details about canopy photosynthesis and tissues' respiration sub-models can be found in Lakso (2006), Lakso and Poni (2005) and Poni et al. (2006).

The model requires two types of inputs: vine descriptions and weather data. To describe the vine, latitude, day of budbreak, number of shoots, number of clusters per shoot, berries per cluster and row x vine spacings are needed. All these inputs come from data obtained in field experiments: the number of shoots was averaged from the sampled vines, as well as the number of clusters per shoot and that of berries per cluster (Table 1). Values of radiation interception, light-saturated photosynthesis rates, quantum yield, extinction coefficient, and temperature responses of organ respiration, leaf area development or photosynthesis, or cultivar specific growth data should be entered either from direct measurements or default values averaged from experimental and literature data. Due to the amount of common canopy manipulation and leaf removal, it is preferred to enter direct measurements of light interception than to model this process with assumptions that are often not met. Therefore, the values of the proportion of light intercepted by the canopy have been obtained from the field measurements made in the experimental vineyards, whereas the values for the remaining inputs (Table 1) have been taken from the literature. The weather daily records required are commonly available:

Table 1
Model input definitions, units and values. These inputs were used for the sensitivity analysis, except for those referring to relative sink strengths (RSS).

Parameter	Value	Units	Description
Number of shoots	15	Shoots vine^{-1}	Number of shoots in the grapevine
Clusters per shoot	1.52	Cluster shoot^{-1}	Number of clusters per shoot
Berries per cluster	212	Berry cluster^{-1}	Number of berries per cluster
LeafDMperArea	88	g m^{-2}	Coefficient to transform leaf dry matter to leaf area.
RSS Wood	0.03	Dimensionless	Relative Sink Strength for wood
RSS Roots	0.03	Dimensionless	Relative Sink Strength for roots
RSS Fruits	0.04–0.9	Dimensionless	Relative Sink Strength for fruits
RSS Shoots	0.04–0.9	Dimensionless	Relative Sink Strength for shoots
Canopy K	0.3	Dimensionless	Extinction coefficient of the canopy
PChemEff	1.9–4.0	μgCO_2 J^{-1}	Leaf photochemical efficiency
LtInt	0–0.42	Dimensionless	Proportion of light intercepted by the canopy over the growing season
Pmax	0–0.001	g CO_2 m^{-2} s^{-1}	Light-saturated photosynthesis under non-limiting conditions

maximum and minimum temperatures, and total radiation. Latitude is required to calculate day-length.

In VitiSim, daily photosynthesis rate (P_n) is calculated using the Charles-Edwards (1982) approach (Lakso et al., 2001; Poni et al., 2006), which is a daily canopy photosynthesis response to daily absorbed radiation. In this version of the model the seasonal fractional light interception is an input rather than being modeled from leaf area as is more commonly done. This was due to the extreme canopy manipulations (shoot positioning, topping, leaf removal) done in grapevines that do not adhere to the assumptions of the common light attenuation models.

The partitioning of the accumulated fixed carbon is adapted from Buwalda (1991) and detailed in Lakso et al. (2001, 2008). In summary, carbon available for partitioning is first calculated as the net CO_2 exchange from canopy photosynthesis (from a daily response curve to intercepted radiation) minus the respiration of all organs to give the available CO_2/dry matter pool. The demands for shoots and clusters at any time are estimated from the number of growing organs multiplied by the estimated maximum growth rates per organ at a given stage. The fractions of growing shoots and clusters are estimated empirically from seasonal measurements of the modeled cultivar and vineyard. Seasonal patterns of root demand are estimated from published results (Comas et al., 2005).

If a sufficient amount of carbon is available to fully support all organs, the carbon is partitioned equal to the demands and maximum growth occurs for all organs. However, if carbon supply is less than the total demand, a prioritization was used. Relative sink strength (RSS) was estimated for each organ type, and the total of the RSS factors equals 1. The rank order was the following: shoots > > fruits > roots = wood = reserves (after 550 °-days). This gave priority to shoots and they received a greater proportion of their demand early in the season. Later, as shoots terminate growth and their demand decreased, the partitioning shifts to fruits, in accordance with field experiments (e.g. Hale and Weaver, 1962; Coombe, 1992).

VitiSim considered reserves as a source or a sink of carbon depending on the phenological stage. The amount of dry weight released by reserves is 485 g (unpublished experiments), which are converted to CO_2, since the carbon balance provided by VitiSim is expressed in g CO_2 as units, assuming that non-structural carbohydrates are mainly composed by glucose (0.68 g glucose / g CO_2). The stock of reserves does not allow negative values. Reserves will be a source only until 15 days after flowering; during this period, they will release all the dry matter needed until they finish (Bates et al., 2002; Smith et al., 2006), in our case those 485 g previously mentioned, whereas Bates et al. (2002) observed a value of 40 g for young vines. After this period, reserves will act as carbon sinks with a potential demand of 125% of the amount of reserves released during the initial part of the season. This would allow for a higher refilling of the reserves pool in those cases of very low sink demand by other organs or very high source capacity.

The amount partitioned to each organ type depends on the individual demands, the number of actively-growing organs, and whether carbon is adequate or limiting (Lakso et al., 2008). The relative partitioning to a given organ (RP_i) is calculated according to the following equation:

$$RP_i = Demand_i - \left(Demand_i \cdot (1 - RSS_i) \cdot \left(1 - \frac{Carbonavailable}{Totaldemand}\right)\right) \quad (1)$$

The actual carbon partitioned then to each organ ($Carbon_i$) is

$$Carbon_i = RP_i \cdot \frac{Carbonavailable}{\sum RP_i} \quad (2)$$

Organ respiration is based on the exponential response of the respiration rate to temperature (Poni et al., 2006). Root respiration was also considered (Lakso et al., 2008). In this case, two sections were taken into account: 1) thick roots and root shank and 2) new fine roots. Structural roots respiration rate (per gram of dry matter of roots) was assumed to be equal to that of the above-ground wood respiration. For new fine root production, the seasonal amount was derived from the carbon partitioning sub-model. Respiration rate equations were those reported by Huang et al. (2005).

2.4. New implementation for accounting for water stress

Water stress reduces P_n (Chaves et al., 2009). In order to account for this reduction, an empirical equation relating Ψ_s and P_n was developed from data measured at midday in the Requena vineyard from 2005 to 2009 (n = 119). First, we calculated the average P_n when Ψ_s was more positive or equal to –0.8 MPa, the threshold for vine photosynthesis responding to water stress (Intrigliolo and Castel, 2011). From this non-stressed average P_n value (12.0 μmol m^{-2} s^{-1}), a fractional ratio between the measured P_n value at a given moment and this average was calculated. This ratio was then plotted against the Ψ_s (Fig. 1a) and the following correction factor was obtained:

$$CorP_n factor = -0.975 \cdot \Psi_s^2 - 1.27 \cdot \Psi_s + 0.57 \quad (3)$$

When Ψ_s is above –0.8 MPa, indicating no stress, no correction is applied. However, when Ψ_s is less than –0.8 MPa (i.e. more negative indicating stress), the P_n rate calculated by the Charles-Edwards (1982) equation is multiplied by the correction factor provided by equation (3), thus accounting for the reduction in photosynthesis caused by water stress. Since this equation accounts only for the effects of mid-day stem water potential on photosynthesis at that time, using it for integrating the effects of water stress on photosynthetic activity over the day will cause an overestimation of these effects.

2.5. Sensitivity analysis and model performance

A sensitivity analysis was performed for the case when no water stress was involved in the simulation in order to identify the model inputs with the greatest influence on dry mass accumulation (total and

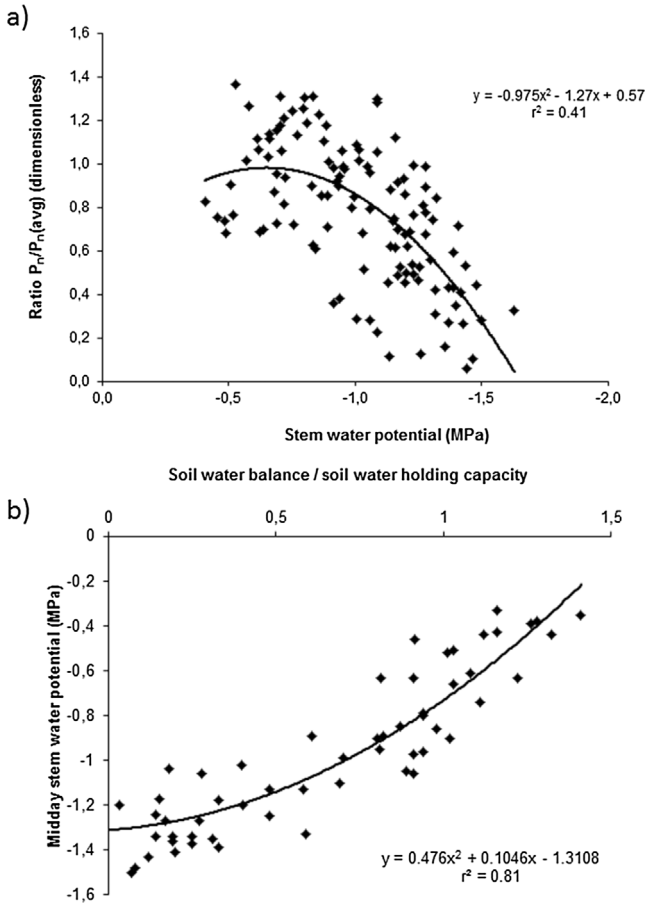
a)
Ratio P_n/P_n(avg) (dimensionless)
y = -0.975x² - 1.27x + 0.57
r² = 0.41
Stem water potential (MPa)
Soil water balance / soil water holding capacity
b)
Midday stem water potential (MPa)
y = 0.476x² + 0.1046x - 1.3108
r² = 0.81

Fig. 1. a) Relationship between midday measurements of stem water potential (Ψ_s) and the ratio between leaf net photosynthesis (P_n) and its averaged maximum when Ψ_s is greater than −0.8 MPa. Values are from the growing seasons 2005 to 2009 at the Requena vineyard. b) Relationship between the ratio soil water balance / soil water storage capacity and Ψ_s. Values are from the growing seasons 2007 to 2009 at Badajoz and Requena vineyards.

in each organ), respiration, photosynthesis and leaf area development over the growing season. The model was considered to be sensitive to an input for a given output when a 20% change in this input led to a variation of at least 5% in the output (Mirás-Avalos et al., 2011). The inputs considered were the extinction coefficient (Canopy K) of the canopy, the number of shoots, clusters per shoot and berries per cluster, the leaf dry mass per area unit (LeafDMperArea), leaf photochemical efficiency (PChemEff), light-saturated photosynthesis under non-limiting conditions (Pmax), and the proportion of light intercepted by the canopy (LtInt). Values and units for these inputs are displayed in Table 1. Since Pmax, LtInt and PChemEff are not constant over the season, their values were either increased or reduced by 20% over the entire season.

In the case of VitiSim, light interception is a direct input and it is not modeled from leaf area; therefore, leaf dry mass per area unit and shoot number are not affecting light interception and photosynthesis.

The performance of the model was assessed using a set of indicators including the Pearson's *r* correlation coefficient between observed and simulated values; the mean absolute error (MAE); the relative root mean square error (RRMSE) and the percentage of bias (PBIAS). These indices have the following expressions:

$$RRMSE = \frac{1}{\bar{O}}\sqrt{\frac{\sum_{i=1}^{n}(P_i - O_i)^2}{n}} \quad (4)$$

$$MAE = \frac{1}{n}\frac{\sum_{i=1}^{n}|P_i - O_i|}{\bar{O}} \quad (5)$$

$$PBIAS = 100 \times \frac{\sum_{i=1}^{n}(O_i - P_i)}{\sum_{i=1}^{n} O_i} \quad (6)$$

Where P_i and O_i are, respectively, the predicted and observed values, n is the number of data pairs, and $\bar{O}$ is the average of the observed values. The optimal value for RRMSE, MAE and PBIAS is zero. In contrast, an r value of 1 expresses perfect agreement between O_i and P_i, whereas zero describes complete disagreement.

2.6. Simulation scenarios

To assess the behavior of the model in different situations, several simulation scenarios were designed.

A first set of scenarios consisted of simulating a "standard" default vineyard, similar to the one located in Requena and described earlier in this document, in a range of areas within the Spanish geography in order to compare vine above-ground dry mass under non limiting water conditions and under the conditions of an average year in each of these locations. For doing this, seven Spanish wine regions, or Designations of Origin (DO), with contrasting climate characteristics were selected: DO Extremadura, DO Jerez, DO La Mancha, DO Rías Baixas, DO Ribera del Duero, DO Rioja, and DO Utiel Requena (Supplementary Fig. 1).

Climate data from 10 years were collected at weather stations located within these areas in order to obtain the average weather conditions for each of them. These data allowed for calculating the length of grapevine growing cycle on each location. A procedure for estimating Ψ_s was developed using a simple soil water balance (SWB, using rainfall as input and crop evapotranspiration as output and considering that soil was at field capacity at the beginning of the growing season) relative to the soil water holding capacity (therefore, our index is dimensionless) based on data registered in Badajoz and Requena for four years (Fig. 1b) ($\Psi_s = 0.476*SWB^2 + 0.1046*SWB - 1.3108$, n = 63, $r^2 = 0.81$, p-value < 0.01), when degree days over the growing season were between 500 and 1500 °C days (base 10 °C). Before 500 °C day, which is approximately the thermal time when pea-size stage is reached, no water stress was considered ($\Psi_s > -0.8$ MPa) due to soil water refilling by springtime rainfall. After 1500 °C day, Ψ_s was considered to vary according to $\Psi_s = SWB - 1.4$, to fit our experimental measures, in order to gradually recover less negative values. For each site, two different scenarios were simulated: i) irrigation (Ψ_s greater than −0.8 MPa over the whole season) and ii) rain-fed (Ψ_s simulated according to the abovementioned procedure). The inputs for the model were equal for each of these locations, except for latitude, day of budbreak, length of the growing cycle, climate variables and Ψ_s.

A second set of scenarios used weather inputs from vineyards in a number of winegrowing areas worldwide. The selection of these locations was made on the basis of data availability and to reproduce contrasting climate conditions. Therefore, climate data for several years were collected at Griffith (New South Wales, Australia), Blenheim (Marlborough, New Zealand), Stuttgart (Baden-Wurtemberg, Germany), Luján de Cuyo (Mendoza, Argentina), and Debrecen (Hadju Bijar, Hungary). Then, an average year was calculated for each location and Ψ_s values for this average year were estimated using the procedure described above. Finally, rain-fed and irrigation conditions (the level of water stress over the season depended on the climate characteristics of each site) were simulated for each site as described for the Spanish scenarios.

Finally, a third set of scenarios took into account the IPCC predictions for temperature and rainfall change (IPCC, 2014). For the period 2046–2065 an increasing in temperature ranging from 0.4 to 2.6 °C is expected as well as decreases in annual rainfall amounts within 5 to 15%. Therefore, for each location, we simulated two possible climate change scenarios: i) a conservative scenario with 1 °C increase in

Table 2
Test of the model against experimental data for 'Tempranillo' grapevines under two different irrigation conditions in two Spanish regions over several seasons.

Year	Treatment	Above-ground dry mass (g)		Fruit dry mass (g)		Leaf dry mass (g)	
		Obs.	Sim.	Obs.	Sim.	Obs.	Sim.
Badajoz (Tempranillo)							
2007	Rain-fed	–	2429.53	–	1286.79	–	636.51
	Irrigated	2004.58	2682.07	909.87	1498.44	334.02	607.86
2008	Rain-fed	2183.74	1718.10	1386.07	882.66	346.46	487.49
	Irrigated	2662.47	2631.09	1718.22	1747.59	384.46	469.57
2009	Rain-fed	899.50	1301.53	464.11	635.70	232.74	290.05
	Irrigated	2670.37	3303.30	1131.03	2062.40	667.86	525.13
2010	Rain-fed	1861.35	1755.49	824.57	908.00	192.26	447.13
	Irrigated	3516.46	3294.54	1225.80	1163.10	762.12	699.86
2011	Rain-fed	1992.81	2372.30	1249.75	1419.39	101.96	576.75
	Irrigated	2164.57	3107.46	1056.43	1837.25	228.09	627.90
Requena (Tempranillo)							
2008	Rain-fed	2848.96	4384.03	1359.99	1452.74	747.79	916.93
	Irrigated	4753.23	5555.63	2361.59	1818.21	1028.84	767.22
2009	Rain-fed	5494.13	3870.14	4267.94	1779.22	740.37	923.09
	Irrigated	6408.66	5272.98	4668.31	2824.88	947.65	975.70

temperature and 5% decrease in rainfall and ii) a worst case scenario with 2 °C increase in temperature and 15% decrease in rainfall. It is acknowledged that the model does not simulate the effects of increased CO_2 concentration that will occur with increasing temperatures. The reductions in rainfall and increases in temperature were performed on long-term average climate data, since we were interested in simulating the effect of a general trend in climate instead of modifying values of a particularly dry year, which would generate more extreme results.

3. Results

3.1. Observed versus simulated data and sensitivity analysis

When compared with data obtained in the seasonal vine growth determinations, VitiSim underestimated above-ground dry masses produced by the vines except for the experiment undertaken in Requena in 2008 and that in Badajoz in 2007, 2009 and 2011, as well as the irrigated plants in Badajoz in 2009 (Table 2). In contrast, fruit and leaves dry masses were overestimated in most cases (Table 2). The differences between observed and simulated above-ground dry mass values ranged from 6% to 45% for the data from Badajoz and between 18% and 54% for the Requena experiment.

Over the growing season, Ψ_s was more negative in the rain-fed vines when compared to the irrigated ones in both locations (Fig. 2). The model calculated differences in photosynthesis between treatments. For instance, in Requena during 2008, Ψ_s differences between treatments were only observed in the summer months and, thus, the dynamics of total photosynthesis was rather similar between rain-fed and irrigated plants (Fig. 3). Greater differences in Ψ_s between treatments were observed in Badajoz, especially in 2008, 2009 and 2010, and, consequently, higher differences in total photosynthesis were simulated by the model (Fig. 3).

The effects of stress on photosynthesis led to differences in accumulated carbon for rain-fed and irrigated vines in the simulations performed. These differences were observed from the day when Ψ_s values were significantly different between treatments and the final decrease in carbon accumulation by the end of the season observed in rain-fed vines was greater, with more negative values of Ψ_s.

In spite of the underestimation in dry masses observed, the correlation coefficients between observed and simulated data were significant and positive, always greater than 0.7 (Fig. 4). In the case of above-ground dry mass, the correlation coefficient was close to 0.85. However, the slopes of the linear regressions were lower than one, indicating that the model underestimates dry mass, especially for fruits and leaves (Fig. 4). The RRMSE was less than 0.5 in the case of above-ground dry mass, almost 0.9 for fruit dry mass and greater than 1.5 in the case of leaf dry mass. Values of MAE were low, ranging from 1.4 to 2.4. In addition, PBIAS only surpassed 15% in the case of leaf dry mass, being less than 12% for fruit dry mass and less than 5% for above-ground dry mass (Table 3).

The inputs that exerted the greatest influence on the model outputs were those related to canopy development and light interception: number of shoots, the extinction coefficient of the canopy (canopy K), the proportion of light intercepted by the canopy over the growing season (LtInt), the leaf photochemical efficiency (PchemEff), the light-saturated photosynthesis under non-limiting conditions (Pmax) and leaf dry matter per area (Table 4). The model was highly sensitive to LtInt, since changes in this input significantly affected the 9 considered outputs. Other inputs such as Canopy K, PChemEff and Pmax influenced 8 out of 9 outputs; number of shoots per vine exerted a significant influence on 5 out of 9 model outputs; LeafDMArea affected 3 of them and, finally, number of clusters and berries per cluster significantly affected 2 model outputs (Table 4).

Above-ground dry mass was very sensitive to changes in those inputs related to sunlight interception and energy conversion (canopy K, LtInt, PChemEff and Pmax). The dry masses of the different plant organs considered here (fruits, shoots, roots, wood and reserves), as well as total photosynthesis, were also significantly affected by changes in the inputs accounting for sunlight interception. Shoot dry matter was least affected by changes in above-ground dry mass due to the higher RSS that stabilized dry mass partitioning in favor of shoot development when the carbon supply was insufficient to support all organs at their demand growth.

Variations in the number of shoots also affected dry masses of different plant compartments (Table 4), when it was reduced by 20%, roots, wood and reserves dry mass values increased more than 22%. Clusters per shoot and berries per cluster variations exerted similar results in the considered outputs (Table 4). Simulated total respiration was only affected by variations in LeafDMperArea and LtInt (Table 4).

3.2. Simulation scenarios

The model simulated different responses for a standard vineyard located at different sites in Spain (Table 5). For instance, the higher dry masses under irrigation conditions were simulated in warm areas such as Jerez de la Frontera (South Spain) and Badajoz (East Spain), whereas the lowest dry mass occurred in cool-humid climates such as that of Lourizán (18% less than in Jerez). However, when rain-fed conditions were considered, vine dry mass values decreased for all locations. Due to differences in rainfall and evaporative demand among regions that

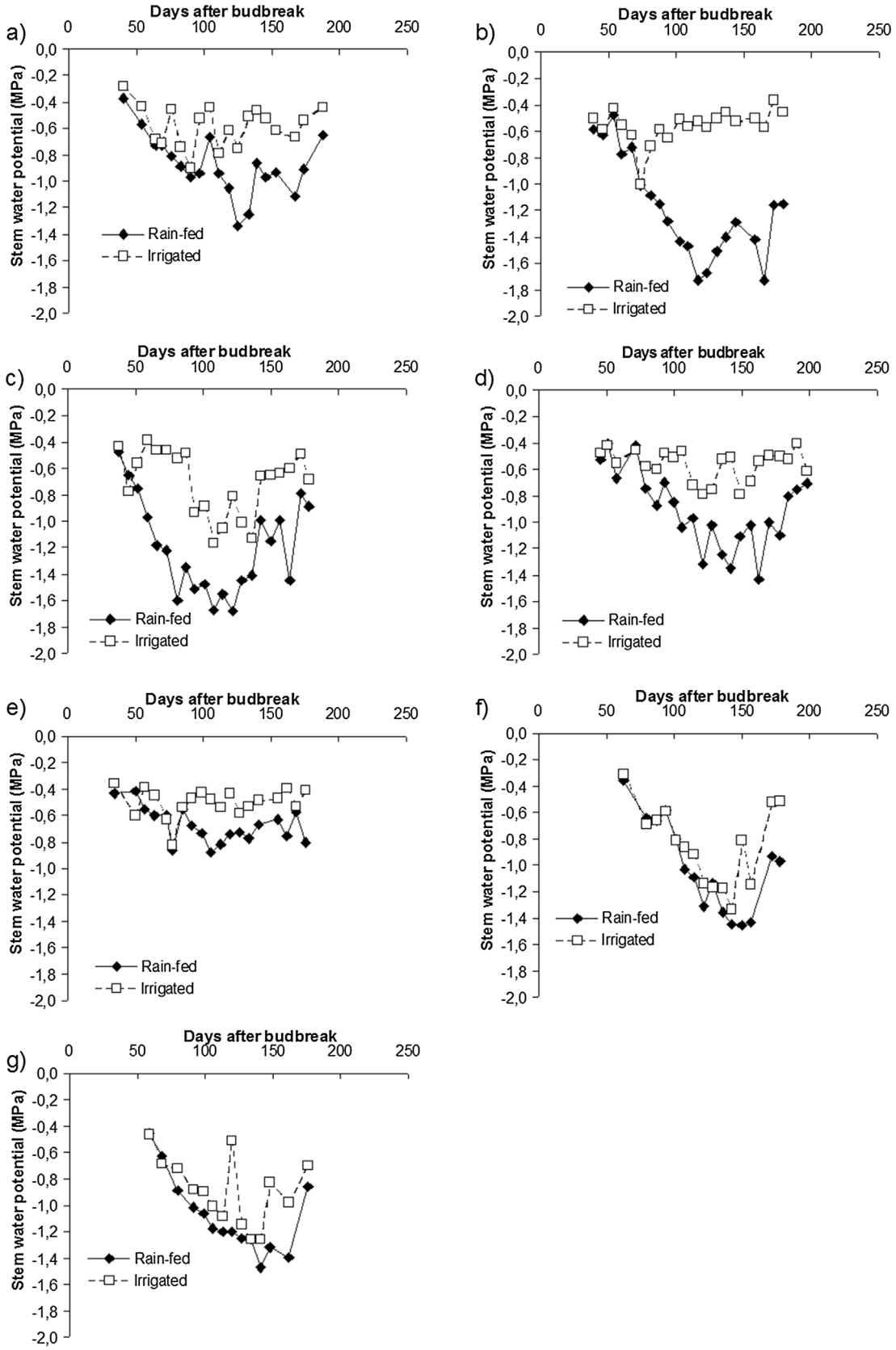

Fig. 2. Seasonal evolutions of the midday stem water potential for rain-fed and irrigated vines measured in the different experiments: a) Badajoz 2007, b) Badajoz 2008, c) Badajoz 2009, d) Badajoz 2010, e) Badajoz 2011, f) Requena 2008, g) Requena 2009.

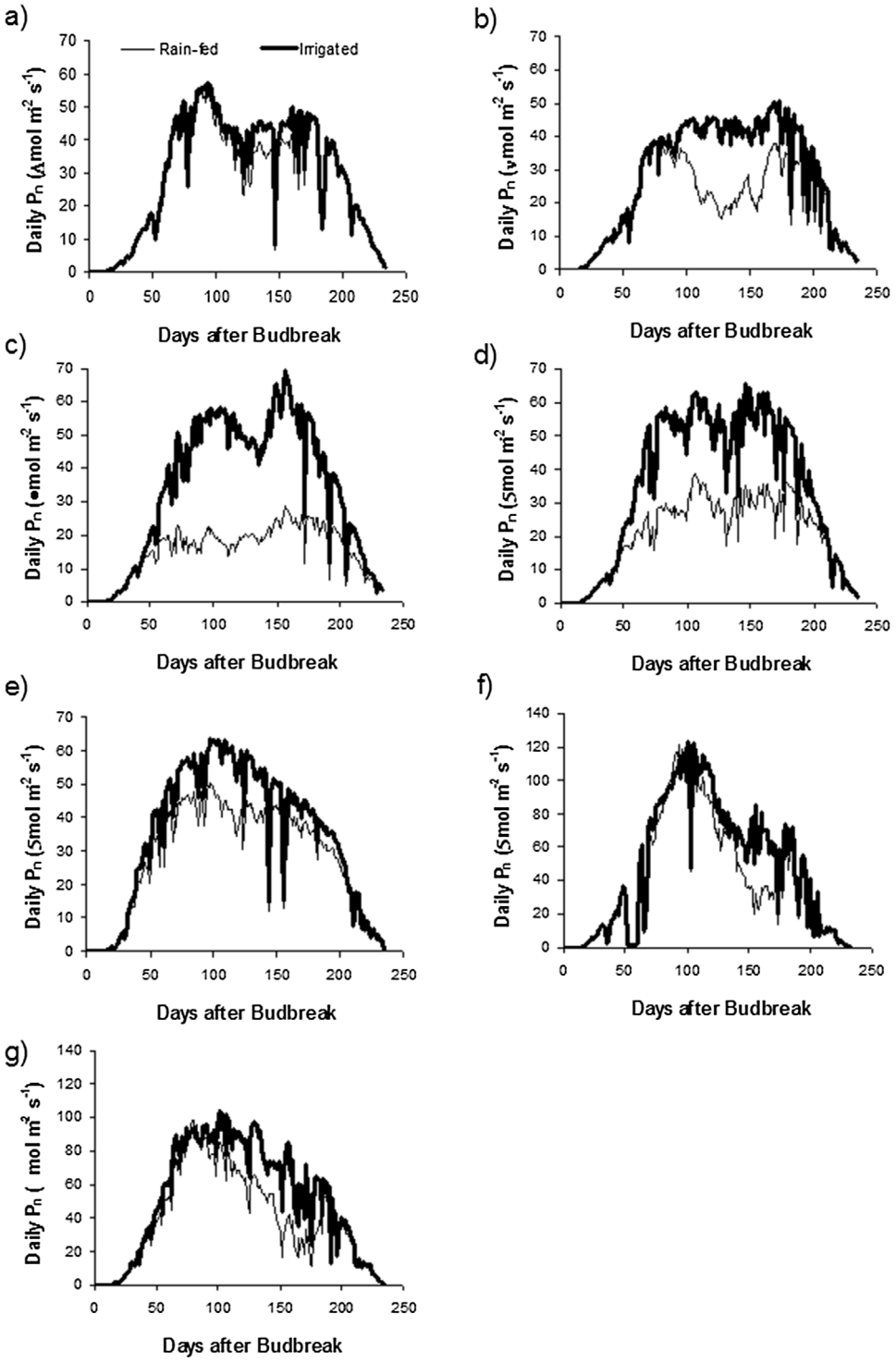

Fig. 3. Simulated seasonal trends of daily photosynthesis for rain-fed and irrigated vines in the different data sets used: a) Badajoz 2007, b) Badajoz 2008, c) Badajoz 2009, d) Badajoz 2010, e) Badajoz 2011, f) Requena 2008, g) Requena 2009.

caused the Ψ_s values to differ among locations, reductions in dry mass due to water stress ranged from 0.4 to 29%. The highest reduction was observed for Albacete (29% loss in dry mass), whereas the lowest one was found for Lourizán (less than 0.5%); which was also the location with the highest dry mass accumulation under rain-fed conditions.

Concerning the international sites, it is noticeable that the simulation for Stuttgart did not show any effects of water restriction under rain-fed conditions and, consequently, vine dry mass was the same for both simulated scenarios (Table 5). Similarly, water restrictions at Blenheim were very low under rain-fed conditions, due to cool climate and sufficient rainfall and the loss of vine dry mass was less than 4%. On the contrary, a high water restriction was observed at Luján de Cuyo under rain-fed conditions, which reduced in more than 32% the vine dry mass when compared to a scenario under no water constraints. The most restrictive case was that of Griffith, were rain-fed conditions led to more than 40% reductions in dry mass. In Hungary, rain-fed conditions reduced simulated vine dry mass production approximately 14% (Table 5).

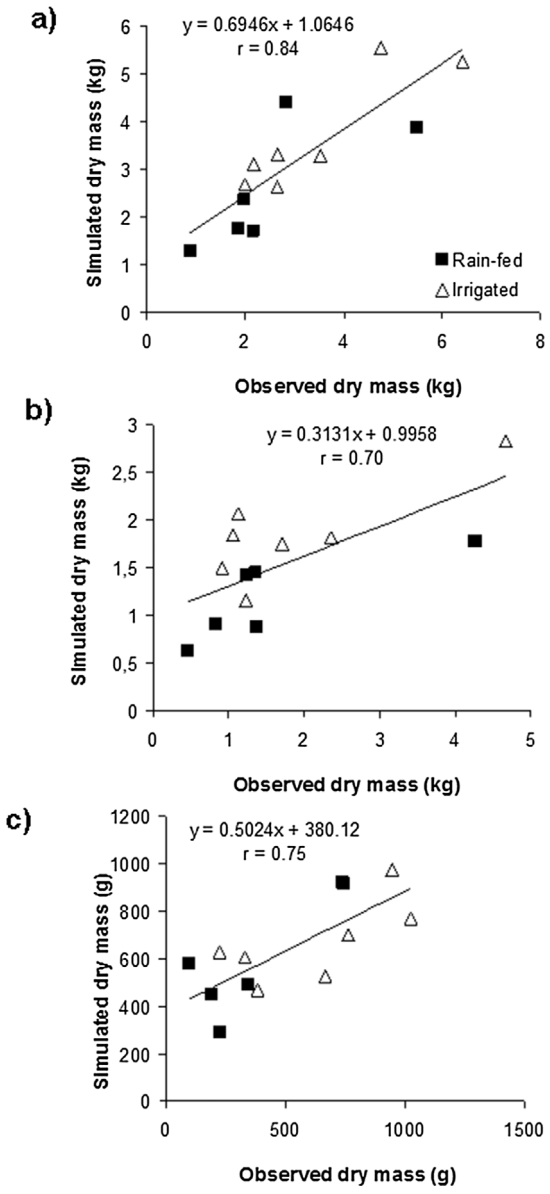

Fig. 4. Relationships between observed and simulated dry masses when all experiments were pooled together: a) above-ground, b) fruit, and c) leaves.

Table 3
Indicators of model performance: *r* Pearson's correlation coefficient; RRMSE, relative root mean square error; MAE, mean absolute error and PBIAS, percentage of bias.

Indicator	Above-ground dry mass	Fruit dry mass	Leaf dry mass
r	0.84	0.70	0.75
RRMSE	0.25	0.93	1.68
MAE	1.42	2.29	2.36
PBIAS	−4.53	11.47	−23.83

In the case of a conservative scenario of climate change, cool regions showed increasing dry masses when compared to those estimated for an average year; whereas those locations with warm and dry climates showed greater reductions in dry mass if only rain-fed (Table 5). For instance, Lourizán, Blenheim and Stuttgart showed 1–5% increases for a conservative scenario, whereas the rest of locations showed decreases in dry mass ranging from 2% (Luján de Cuyo) to 24% (Badajoz and Requena). The same trend was observed when a worst case climate change scenario was simulated, 2% increases in dry mass were estimated for cool-climate locations (Lourizán, Blenheim and Stuttgart), whereas decreasing dry mass (ranging from 8 to 28%) was predicted for warm and hot climate locations (Table 5).

4. Discussion

Despite its simplicity and low input requirements, VitiSim was able to simulate dry mass variations due to differences in vine water status, which is known to diminish plant photosynthesis (Chaves et al., 2009; Tardieu, 2013). The model was useful for simulating vine dry mass production, as indicated by the goodness-of-fit indicators, under a range of conditions using easily available data, most of them concerning climate variables such as temperature or solar radiation. Climate is the dominant factor for vine growth and grape development, with changes in climate and variability influencing phenology, yield and berry composition (Jones and Davis, 2000; Ramos et al., 2015). Future projections in climate indicate potential shifts northwards in European areas suitable for wine production and traditional rain-fed areas in southern Europe may have to adopt irrigation practices to maintain production at current levels (Santos et al., 2012). Hence, the information provided by VitiSim could be useful for estimating the suitability of a given area for grape production or to aid as a tool in decision support systems when programming viticultural practices in the mid-term.

As pointed out by Poni et al. (2006), a sensitivity analysis was carried out in order to understand what inputs would exert a greater influence on the model outputs. The seasonal dry masses of the different organs were very sensitive to changes in the values of inputs dealing with light interception, indicating that their estimation is of paramount importance for obtaining reliable and useful simulation outputs. This might be a potential point of criticism since the values of these inputs are not easily obtained. In our case, light interception measurements were taken in the experiments of Badajoz and Requena on three different dates per season and, probably, additional measurement dates would be advisable to get a more detailed and reliable pattern of this variable over the growing season. Modeling light interception with common light attenuation models, however, is not very accurate in discontinuous canopies, especially with severe restrictions of the canopy form as often seen in vines with vertical shoot positioned training that utilizes hedging and leaf removal.

Furthermore, the sensitivity analysis showed the non-linear response of several processes in the model with respect to the variation in the values of the inputs (Table 4), suggesting the existence of interactions among the different sub-models within VitiSim. For instance, increasing light interception by 20% produced a 29% increase in above-ground dry mass; this might reflect the fact that the proportion of light intercepted during the mid-season, when these values were greater, induced more dry matter accumulation. In addition, a 20% increase in LeafDMperArea results in a 15% reduction in leaf area, which may be due to a difference in the accumulation of dry matter in the shoots.

The results from the simulations indicate that, as reported by field experiments under a range of soil and climate conditions (e.g. Intrigliolo et al., 2012; Picón-Toro et al., 2012; Lanari et al., 2014), water restrictions exerted a strong influence on the final fruit and leaf dry mass, as simulated by the model. However, it must be considered that the factor for correcting photosynthesis rate due to water stress was developed using midday stem water potential readings. Therefore, they might be overestimating the daily effect on P_n to a certain extent, as in the morning leaf water potential is not as negative, as observed in many field studies (Intrigliolo and Castel, 2007; Dinis et al., 2014). Moreover, another limitation of the model is that if the stress occurs early enough in the season, the light interception will be reduced by a decrease in canopy leaf area even if there is no effect on P_n rate per unit of leaf area, which is not considered by VitiSim. If the stress only occurs after shoot growth has stopped then using limitations on P_n rate alone is a reasonable approach.

In addition, VitiSim did not perform well for fruit dry masses since

Table 4
Model sensitivity to the considered parameters.

Parameter	Variation	DM above-ground	DM shoots	DM fruit	Leaf area	DM roots	DM wood	DM reserves	Total respiration	Total photosynthesis
Nº shoots	20%	−2.99	**8.90**	−0.88	**8.80**	**−13.78**	**−13.79**	**−24.47**	3.48	0.00
	−20%	2.91	**−9.82**	0.55	**−9.93**	**22.25**	**22.23**	**24.47**	−3.34	0.00
Clusters per shoot	20%	0.41	−3.09	1.67	−3.18	**−5.86**	**−5.84**	0.00	−0.71	0.00
	−20%	−0.56	4.12	−2.27	4.12	**8.41**	**8.36**	0.00	0.96	0.00
Berries per cluster	20%	0.41	−3.09	1.67	−3.18	**−5.86**	**−5.84**	0.00	−0.71	0.00
	−20%	−0.56	4.12	−2.27	4.12	**8.41**	**8.36**	0.00	0.96	0.00
LeafDMper Area	20%	3.27	2.07	2.57	**−14.98**	3.22	3.21	**3.94**	**−5.44**	0.00
	−20%	−4.68	−3.03	−3.61	**21.16**	−4.49	−4.50	**−5.91**	**7.83**	0.00
Canopy K	20%	**−13.10**	**−6.96**	**−10.67**	**−7.12**	**−10.72**	**−10.74**	**−16.31**	−3.65	**−9.20**
	−20%	**16.11**	**8.46**	**12.93**	**8.43**	**14.72**	**14.70**	**20.76**	4.55	**11.32**
PChemEff	20%	**13.13**	**5.72**	**11.99**	**5.62**	**9.81**	**9.78**	**11.34**	3.11	**8.97**
	−20%	**−15.98**	**−7.22**	**−14.48**	**−7.30**	**−11.20**	**−11.22**	**−14.30**	−3.85	**−10.95**
LtInt	20%	**28.86**	**13.76**	**24.77**	**13.67**	**24.85**	**24.83**	**30.91**	**7.51**	**20.00**
	−20%	**−28.85**	**−14.31**	**−24.85**	**−14.42**	**−20.80**	**−20.79**	**−30.91**	**−7.47**	**−20.00**
Pmax	20%	**13.17**	**6.93**	**10.59**	**6.93**	**11.93**	**11.90**	**16.92**	3.72	**9.25**
	−20%	**−16.00**	**−8.51**	**−13.06**	**−8.61**	**−12.95**	**−12.96**	**−19.86**	−4.45	**−11.23**

Variations are expressed as a percentage of the reference value on the basis of a ± 20% variation of each model parameter. Variations greater than 5% are indicated in bold.
Canopy K = extinction coefficient of the canopy; LtInt = proportion of Light Intercepted by the canopy; DM = Dry Mass; PChemEff = Leaf Photochemical Efficiency.

the model underestimated fruit dry mass when compared to the field observations. Underestimations were larger for higher values of dry mass. This was likely caused by the fact that the rule adopted for carbon partitioning among reproductive and vegetative organs was not optimal and could be improved.

The designed simulation scenarios allowed us to compare climatic potentials, namely a “standard” vine was used for modelling the effects of climate conditions from several locations depending only on rainfall, producing realistic results. For instance, sunny, warm and hot climates, such as those from Badajoz and Jerez de la Frontera in Spain and Griffith in Australia, showed that these locations have a greater potential for dry matter production than cool climates such as those from northwest Spain, Germany or Hungary if water is not limiting. This is likely due to greater solar radiation values, on the warmer locations, that would cause differences in daily canopy photosynthesis in the mid-season. In fact, seasonal simulated dry matter was strongly correlated with the solar radiation amount during the season ($r = 0.96$, p-value < 0.01). In addition, temperature may have a relevant effect since it changes the length of grapevine growing cycle (from budbreak to leaf fall); this has been accounted for when positioning an standard vineyard on each location and growing cycle varied between 220 and 260 days depending on the site. Our results suggest that VitiSim performs reasonably well for estimating dry matter production in grapevines grown under Mediterranean and oceanic climates. The success in the applicability of VitiSim to other wine regions, such as those on continental climates, would depend on the accuracy in determining the inputs concerning light interception by the canopy and photosynthetic efficiency of the grapevine varieties growing there as well as considering the length of their growing cycle. In this sense, the simulations performed using weather data from continental climates, such as those from Hungary and Germany, suggest that VitiSim can provide realistic information about grapevine dry matter production.

Furthermore, the results from these simulations are in agreement with those by Maxwell et al. (2015), who projected grapevine growth and yield decreases and considered that these would have large implications for wine industry, especially to growers that would require

Table 5
Simulations of above-ground vine dry mass seasonal gain for a standard vineyard situated in different locations within Spain and other wine producing regions in the world as a function of non-limiting water, rain-fed conditions and under two different climate change scenarios: Conservative (increasing of temperature by 1 °C and 5% decrease in rainfall) and Worst case (increasing of temperature by 2 °C and 15% decrease in rainfall). The percentages displayed are those over the irrigation conditions (midday stem water potential less negative than −0.8 MPa for the whole season), for the case of the rain-fed scenario (midday stem water potential estimated for the weather conditions of an average year in the given location), and those over the rain-fed conditions in the case of the climate change scenarios. Data on rainfall, reference evapotranspiration (ET_0) and solar radiation over the growing season of an average year are also provided for each location.

			Growing season (budbreak to leaf fall)			Seasonal above-ground dry mass gain (g)			
Site name	Location	Latitude	Rainfall (mm)	ET_0 (mm)	Solar radiation (MJ m^{-2})	Irrigation	Rain-fed	Conservative	Worst case
Spanish wine producing regions									
Albacete	La Mancha	38.95 °N	207.0	1047.3	4730.2	3443	2457 (71%)	2334 (95%)	2266 (92%)
Badajoz	Extremadura	38.86 °N	311.6	1117.5	5225.6	3764	2718 (72%)	2059 (76%)	1963 (72%)
Jerez de la Frontera	Jerez	36.64 °N	363.5	1126.9	5437.3	3789	2747 (73%)	2642 (96%)	2478 (90%)
Logroño	Rioja	42.44 °N	306.3	919.4	4236.4	3262	2703 (83%)	2096 (78%)	2092 (77%)
Lourizán	Rías Baixas	42.41 °N	966.6	862.9	4014.5	3207	3195 (99%)	3221 (101%)	3241 (102%)
Requena	Utiel-Requena	39.51 °N	284.1	917.5	4745.9	3463	2771 (80%)	2098 (76%)	2093 (76%)
Zamadueñas	Ribera del Duero	41.70 °N	238.7	881.3	4353.4	3291	2677 (81%)	2290 (86%)	2288 (85%)
World wine producing regions									
Stuttgart	Baden-Württemberg (Germany)	48.78 °N	500.8	971.6	3072.0	2378	2378 (100%)	2514 (106%)	2424 (102%)
Luján de Cuyo	Mendoza (Argentina)	33.00 °S	229.4	1012.5	4620.0	3305	2216 (67%)	2169 (98%)	2039 (92%)
Griffith	New South Wales (Australia)	34.29 °S	289.8	1098.2	5046.5	3424	1999 (58%)	1914 (96%)	1788 (89%)
Blenheim	Marlborough (New Zealand)	41.50 °S	321.3	781.4	4252.2	2896	2805 (97%)	2879 (101%)	2801 (100%)
Debrecen	Hajdú-Bihar (Hungary)	47.36 °N	364.9	1062.6	2718.4	2337	2016 (86%)	1931 (96%)	1802 (89%)

the establishment of irrigation systems, increasing the cost of growing grapes. Based on general experience, the varying climate change scenario simulations provided realistic results about the effects of increasing temperatures and decreases in total rainfall amounts on the accumulation of dry mass by the vines in different locations. Scientific reports about dry mass accumulation at the whole grapevine level do not abound, and they usually refer to different cultivars, so comparing the results from our simulations with field data is a difficult task. Castelan-Estrada et al. (2002) working on Merlot cultivar in Bordeaux (approximately, 1000 mm rainfall per year) found above-ground dry masses ranging from 1050 to 1550 g per vine, depending on soil management. Scandellari et al. (2016) found, for Carmenère cultivar, in North Italy (830 mm rainfall and 1142 mm ET_0 per year) an above-ground dry biomass close to 771 g per vine. Finally, Miranda et al. (2017), using allometric relationships, reported data for four cultivars (Cabernet Sauvignon, Grenache, Marselan and Tempranillo) and indicated that above-ground dry biomass varied between 2300 and 3500 g per vine, depending on the cultivar and the location, as they studied five locations within Spain. Our simulations showed values within those ranges but also some overestimations depending on irrigation in the vineyard and the year studied. Therefore, it seems that VitiSim gave reasonable estimations of dry matter accumulation in the above-ground organs of the grapevine.

A limitation of the current model is the empirical equation used to account for the effect of water deficit on grapevine. Further work is needed to overcome this drawback and include solid algorithms for calculating those relevant issues, since intercepted solar radiation is linearly correlated with whole-canopy net CO_2 exchange rate (Petrie et al., 2009) and vine canopy development is very sensitive to water stress (Chaves et al., 2009). Moreover, despite the variations in Ψ_s, the partitioning coefficients were held constant in VitiSim. However, the absolute C partitioning would change as it varies with full C supply to total demand versus conditions of C deficits that lead to more relative partitioning to stronger sinks, such as shoots and fruits (Bota et al., 2004). Due to its simplicity, VitiSim was not able to account for this possible change in C partitioning coefficients, which may also vary depending on the time of occurrence of water stress over the growing season. These issues are still a matter of debate when modeling C allocation in fruit trees and vines (Génard et al., 2008).

Another limitation is the fact that phenology is indirectly accounted for in VitiSim and the timing of budbreak is not modeled. Some of the variables simulated by the model consider phenological stages as a function of growing degree days; however, user must input the length of the cycle and the day of budbreak to initiate the simulations. Therefore, VitiSim users must enter budbreak dates if simulating past seasons and consider other models to simulate a warming and drying of the growing season in the Mediterranean (Fraga et al., 2016) as well as the lengthening of growing seasons and earlier phenological events (Ruml et al., 2012), which may lead to earlier and unbalanced ripening (Webb et al., 2011).

Finally, the results from the current study demonstrated that this simplified dynamic modelling approach might help to integrate existing data and focus future research efforts on the defined key features affecting vine carbon balance. In addition, the carbon balance model can be useful to understand and optimize interactions of vine physiology with environment and management.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.scienta.2018.06.065.

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